Proboscis and foregut morphology of *Ficus subintermedia* (d'Orbigny, 1852) (Caenogastropoda: Ficidae)

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ABSTRACT

Fig shells (Ficidae) have been identified as a putative sister group to Neogastropoda, although they have historically been associated with Tonnoidea. This study examines the morphology of the proboscis and foregut of *Ficus subintermedia* (d'Orbigny, 1852) and compares its major features to those of Neogastropoda and Tonnoidea. The elongate ficid proboscis is operated by an unusual arrangement of proboscis retractor muscles that connect to the esophagus and form a sheath around the proboscis. It appears that the proboscis can not be fully everted and is a functional analogue of an intraembolic proboscis, although this requires confirmation by observation of living animals. The salivary glands are shown to be superficially bilobed but histologically uniform, and the esophageal gland is minimally septate and confluent with the esophagus. Despite a morphologically complex alimentary system, there are few synapomorphies uniting Ficoidea with either Tonnoidea or Neogastropoda.

Additional keywords: Ficoidea, histology, anatomy, alimentary system, intraembolic proboscis

INTRODUCTION

The Ficidae, or fig shells, are a small family of marine caenogastropods that occupy benthic habitat across a global, mainly tropical, distribution. Despite their relatively large body size, moderate abundance and putative relationship to other well-studied caenogastropods, very little is known of the anatomy, systematics, life history, behaviour, or ecology of ficid species. The family Ficidae Conrad, 1867, was established exclusively for the genus *Ficus* Röding, 1798, within Tonnoidea. The subsequent systematic history of the group includes recognition of the superfamily Ficoidea Meek, 1864, the affiliation of Thalassocynidae Riedel, 1994 (containing *Thalassocyon* Barnard, 1960 [Beu, 1969]) with Ficoidea and the description of several ficid fossil genera (see Riedel, 1994).

Only a handful of studies have examined ficid morphology. Excluding descriptions of the shell, superficial examinations of the alimentary system (Amaudrut, 1898; Riedel, 1994), external morphology (Arakawa and Hayashi, 1972), mantle (Liu and Wang, 1996), nervous system (Bouvier, 1887) and radula (Warén and Bouchet, 1990; Riedel, 1994) are scattered throughout the literature. These data suggested to some reviewers (Warén and Bouchet, 1990; Riedel, 1994) that Ficoidea are morphologically distinct from Tonnoidea, but are insufficient to establish their relationship with other groups of caenogastropods.

The position of Ficidae within Caenogastropoda was examined by a combined morphological and molecular analysis (Riedel, 2000), which suggested Ficidae may be a sister taxon to Neogastropoda, united by features such as egg mass morphology, radular configuration, concentration of the circumesophageal nervous system, and operation of the proboscis. A more recent phylogeny of Caenogastropoda, using morphological data, placed Ficidae outside a large clade including the predatory groups Neogastropoda, Tonnoidea, and Cypraeoidea (Ponder et al., 2008). However, both these analyses were based on minimal and uncorroborated descriptions of ficid anatomy.

The internal relationships and evolution of Neogastropoda are a topic of considerable interest (Ponder, 1974; Taylor and Morris, 1988; Kantor, 1996; Harasewych et al, 1997; Kantor, 2002), but there is uncertainty surrounding the identity of extant sister taxa, the resolution of which would greatly assist in resolving internal neogastropod relationships by polarizing key morphological characters. Previous morphological studies have indicated that Ficoidea (Riedel, 2000), Tonnoidea (Graham, 1941; Ponder et al., 2008), a lower caenogastropod (Ponder, 1974; Golikov and Starobogatov, 1988), an epitoniid (Strong, 2003) or an underived carnivorous sorbeoconch (Kantor, 2002) is most closely related to Neogastropoda. There may be multiple sister taxa, as some authors consider Neogastropoda paraphyletic (see review by Taylor and Morris, 1988).

Further information on the morphology of Ficidae will be valuable in determining if they have synapomorphies which unite this group with either Neogastropoda or Tonnoidea. This study describes aspects of the anatomy and histology of *Ficus subintermedia* (d'Orbigny, 1852). The study focuses on the proboscis and foregut, as these structures are particularly informative in

defining groups of higher caenogastropods, including Neogastropoda.

MATERIALS AND METHODS

Specimens of *Ficus subintermedia* were obtained from the Australian Museum collections (C.353111). The specimens were collected by I. Loch at Cairns Reef, Queensland, Australia (15°42′ S, 145°30′ E) on 27 July 1973 and preserved in 5% formalin. Two male specimens were dissected under a stereo microscope and illustrated using a camera lucida. A third male specimen was post-fixed for 24 h in Bouin's fluid, dehydrated and saturated with Paraplast ™ paraffin using a Tissue-Tek ® VIP tissue processor. The embedded specimen was serially sectioned at 7 μm using an American Optical microtome. Mounted sections were stained using Cason's trichrome (acid fuchsin, aniline blue, and orange G) and Mayer's haematoxylin. Photographs of the sections were obtained using an Olympus DP70 digital camera mounted on an Olympus BX50 microscope.

The proboscis, salivary gland, jaws, and radula were removed from dissected specimens for scanning electron microscopy (SEM). The soft-tissue samples were dehydrated to 100% EtOH and critical point dried using a Bal-Tec CPD030. The radula was cleaned overnight using warmed NaOH to remove buccal tissue. The samples were sputter-coated with gold and examined using a Zeiss Evo LS15 SEM with a Robinson backscatter detector.

RESULTS

GENERAL FOREGUT MORPHOLOGY: Foregut dominated by extremely long proboscis, ~2–3 times anterior esophagus length (from esophageal gland to buccal mass) (Figures 1–3, **pb**). Concentrated circumesophageal nerve ring anchors esophagus to pedal musculature anterior to esophageal gland. Introverted proboscis forms loop leading posteriorly through haemocoel to small buccal mass (Figure 2). Proboscis folded to occupy most of haemocoel, fused to lateral walls of head and foot at base of neck (Figure 3). Walls of slender neck form rhynchodeum with rhynchostome at tip (Figure 1, **rh**). Pair of large, tapering cephalic tentacles present on rhynchodeal wall; with subdermal, pigmented eyes at base (Figure 1, **ey, te**).

PROBOSCIS: Fully introverted proboscis forms 'acrembolic' arrangement (Fretter and Graham, 1962); buccal mass and esophagus situated posterior to distal tip of proboscis (Figure 2). Walls of proboscis relatively thin (Figure 4, **pw**). Pair of nerves run laterally along internal surface of proboscis wall (=outer surface when introverted), each embedded in narrow sheet of circular muscle fibers that joins proboscis wall in two places (Figures 4, 5, **pn, cm**). When introverted, lateral proboscis wall pinched off by sheet of circular muscle to form two longitudinal flaps (here termed 'proboscis folds')

which project into lumen of introverted proboscis (Figures 2, 4, 7, **pf**). Proboscis folds flattened when proboscis is everted; sheet of circular muscle stretched to accommodate greater circumference (Figure 8). Exterior surface of proboscis wall (=interior surface when introverted) covered with papillose epithelium, tallest on ventral surface, reduced in height on apex of each proboscis fold (Figures 7–9, **pa**). Each papilla approximately 50 μm in diameter, dotted with pores on tip (Figure 9). Histology of papillae composed of mucus cells opening to each pore, below extracellular cuticle layer.

Pair of large retractor muscles attach to proboscis, anchor to lateral body walls (Figures 2, 3, **prm**). Proboscis retractor muscles short, fused to interior part of proximal proboscis wall near connection to rhynchodeum. Separate branch from each retractor muscle also connects to esophageal wall where it loops towards anterior of haemocoel to pass anterior to circumesophageal nerve ring (Figures 3, 6). Junction between proboscis retractors, esophagus situated approximately midway between esophageal gland and buccal mass (immediately anterior to circumesophageal nerve ring). Branches of retractor muscles extend anteriorly as two flattened sheets of longitudinal muscle sheathing dorsal, ventral surfaces of esophagus, buccal mass, salivary gland ducts, nerves situated near esophagus (Figures 2–6, **prm**). Near proximal proboscis base, retractor muscles taper off, fuse to inner wall of proboscis (Figure 3).

BUCCAL MASS AND RADULA: Buccal mass short, slightly wider than adjacent esophagus, proboscis (Figure 2, **bm**). Odontophoral retractor muscles derived from buccal mass inserted into proboscis retractor muscle covering esophagus. Pair of elliptical jaws present on dorsal surface of anterior buccal mass (Figure 2, **ja**). Jaws prismatic, composed of parallel rods (Figure 10).

Radula taenioglossan, similar to those figured by Riedel (1994) and Warén and Bouchet (1990) (Figure 11). Central tooth triangular, with large median cusp flanked on each side by six or seven secondary cusps (Figure 12). Each lateral tooth with major cusp directed centrally, single inner cusp, approximately 6 outer cusps of decreasing height. Both marginal teeth elongate, hook-shaped, inner marginal tooth differentiated with row of small cusps on outer edge (Figure 12).

ANTERIOR ESOPHAGUS: Epithelium lining anterior esophagus folded, without any prominent or persistent longitudinal folds (Figures 13, 14, **oe**). No distinguishable dorsal, ventrolateral folds in posterior buccal mass or elsewhere in esophagus. Muscular esophageal wall composed of internal layer of ciliated columnar epithelium with occasional mucus cells, layer of longitudinal muscle, thick exterior layer of circular muscle (Figures 6, 13, 14).

ESOPHAGEAL GLAND: Posterior to nerve ring, esophagus expands to form esophageal gland (Figure 2, **og**). Histological sections through gland show epithelium not well preserved, but condition sufficient to determine main morphological aspects. Interior of gland dominated by
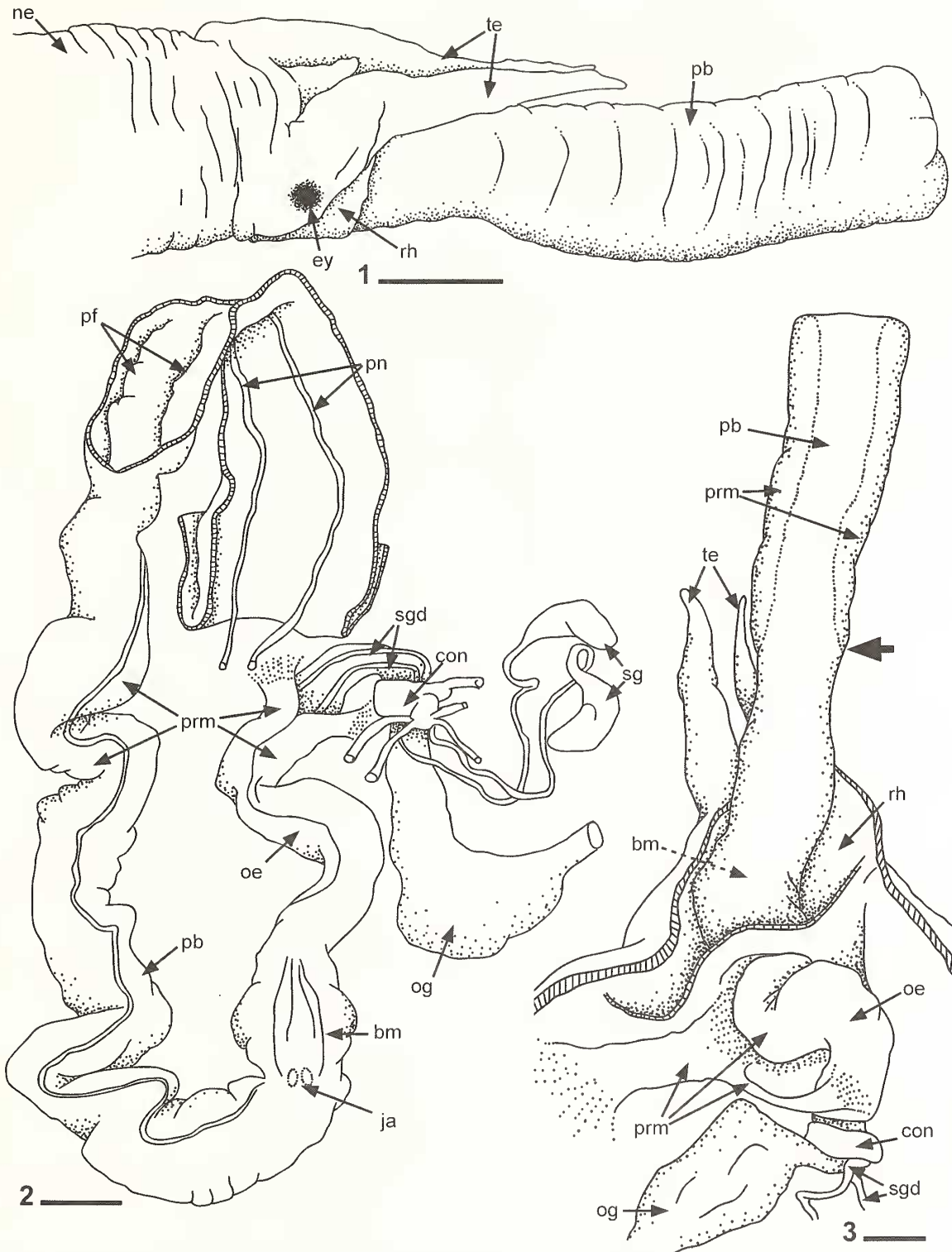
Figures 1–3. Illustrations of the foregut of *Ficus subintermedia*. **1.** Lateral view of head and partially everted proboscis. **2.** Introverted proboscis, esophagus and salivary glands, with proximal proboscis wall dissected open to show pseudo dorsal folds. **3.** Dorsal body wall dissected open to show foregut and partially everted proboscis, with anterior insertion of proboscis retractor muscles indicated by large arrow and position of buccal mass indicated by dashed arrow. Abbreviations: **bm**, buccal mass; **con**, circumesophageal nerve ring; **ey**, eye; **ja**, jaws; **ne**, neck; **oe**, esophagus; **og**, esophageal gland; **pb**, proboscis; **pf**, proboscis fold; **pn**, proboscis nerve; **prm**, proboscis retractor muscle; **rh**, rhynchodeum; **sg**, salivary gland; **sgd**, salivary gland duct; **te**, cephalic tentacle. Scale bars = 2 mm.

open lumen (Figure 15, **lu**). Branched folds of tissue, derived from gland walls, protrude into lumen (Figure 15, **se**). Epithelium lining of esophageal gland not tall or brightly stained, cells do not appear to contain obvious proteinaceous secretions. Ventral wall of esophageal gland distinguishable only as region with relatively few branching folds (Figure 15). Esophageal gland not separated from esophagus, lacking identifiable dorsal folds in this region or in posterior esophagus.

SALIVARY GLANDS: Pair of small salivary glands, connected to buccal mass by very long ducts (Figure 2, **sg**, **sgd**); composed of two equally sized lobes joined by continuous lumen (Figures 16, 17). Interior of glands convoluted, tubular pockets, each lined by small secretory cells containing large, darkly stained nuclei (Figure 17). No histological differences between anterior and posterior lobes of salivary glands. Pair of narrow salivary gland ducts pass through nerve ring with esophagus, anterior blood vessel (Figure 14), continued anteriorly along lateral surfaces of esophagus, sheathed by branches of proboscis retractor muscles (see above) (Figure 6). Salivary gland ducts insert into dorsal wall of middle part of buccal mass. Anterior section of salivary gland ducts covered by external layer of longitudinal muscle, but not fused to lateral esophageal walls (Figure 14).

DISCUSSION

CONFIGURATION OF THE FICID FOREGUT: The arrangement of the proboscis, retractor muscles, buccal mass and esophagus of *Ficus subintermedia*, and possibly other Ficidae, is unique in Caenogastropoda and is not shared with any other proboscis-bearing group. The extremely long ficid proboscis superficially resembles the equally long proboscis of personids such as *Distorsio* (Lewis, 1972). However, the foregut morphology of Personidae is tonnoidean (with the exception of the lack of acid-secreting proboscis glands). The proboscis of *Distorsio* is not acrembolic when introverted, but is instead retracted (i.e., not turned inside out) and coiled within the rhynchodeum (Lewis, 1972) in a fashion similar to that described for the species of the ranellid *Argobuccinum* (Day, 1969).

Although the introverted ficid proboscis is acrembolic, it is twice the length of the esophagus (Figures 2, 3), which places a physical limitation on the distance that the buccal mass can be everted anteriorly. A simple calculation of the relative lengths (excluding the elastic properties of the esophageal and proboscis walls) suggests that the buccal mass cannot be protruded beyond the level of the rhynchodeum and almost certainly cannot extend to the tip of the everted proboscis as hypothesized by Riedel (1994) (Figures 18, 19). The everted ficid proboscis appears to form a double-walled tube which funnels ingested material toward the buccal mass positioned at its base, with the proximal half of the proboscis effectively an elongated oral tube (Figure 18).

This hypothesis requires confirmation through observation of the feeding behaviour of living ficids, as the mechanism or mechanisms for prey capture in this group are unclear.

A feature supporting the interpretation of proboscis operation outlined above is the longitudinal folds that line the interior of the introverted proboscis. These proboscis folds bear a structural resemblance to the esophageal dorsal folds found in the many caenogastropods including tonnoids and most neogastropods (Graham, 1941; Strong, 2003; Andrews and Thorogood, 2005), but which were absent in the esophagus of *Ficus subintermedia*. Unlike the esophageal dorsal folds, the ficid proboscis folds are temporary and double-walled. Their presence is conditional on the introversion of the proboscis. When the proboscis is everted and the circumference increases, the folds are flattened, which prevents the appearance of the folds on the exterior of the proboscis (Figure 8). Although the position of the ficid proboscis clearly indicates that they are not homologous to esophageal dorsal folds, their convergent evolution suggests that separation of dorsal and ventral lumens confers a strong advantage for the movement of food through the digestive tract. The peculiar papillose epithelium lining the introverted proboscis is dotted with pores which suggest an excretory or absorptive function.

In the scenario described above, the buccal mass is positioned at the base of the proboscis temporarily during feeding (Figure 18). This arrangement superficially resembles some conoideans, which have a buccal mass fixed at the proboscis base—a defining feature of Conoidea which is present in all basal taxa (Taylor et al., 1993) (Figure 22). The highly unusual connection between the proboscis retractor muscles and the esophagus/buccal mass of *Ficus subintermedia* is also found in some conoideans, such as the Terebridae (Simone, 1999) (Figure 22). This evidence is insufficient to conclude homology of the ficid proboscis with the intraembolic proboscis found in some conoidean groups, but it may illustrate a path through which the intraembolic proboscis could have evolved. Retention of the buccal mass at the base of the proboscis during feeding may represent an intermediate step between an acrembolic proboscis and the permanent fixture of the buccal mass at the proboscis base (intraembolic). An alternative derivation of the intraembolic proboscis from the pleurembolic form, widely occurring in Muricoidea and Cancellarioidea, was presented by Simone (1999, fig. 27), who showed that the intraembolic proboscis is an elongation of the buccal region. These conflicting theories could be resolved by the development of a robust phylogeny of Neogastropoda.

RELATIONSHIP OF FICIDAE TO TONNOIDEA AND NEOGASTROPODA: Riedel (1994) listed four morphological features shared by Ficidae and Neogastropoda. The egg mass and the configuration of the nervous system were not addressed in this study, but states of the radula and
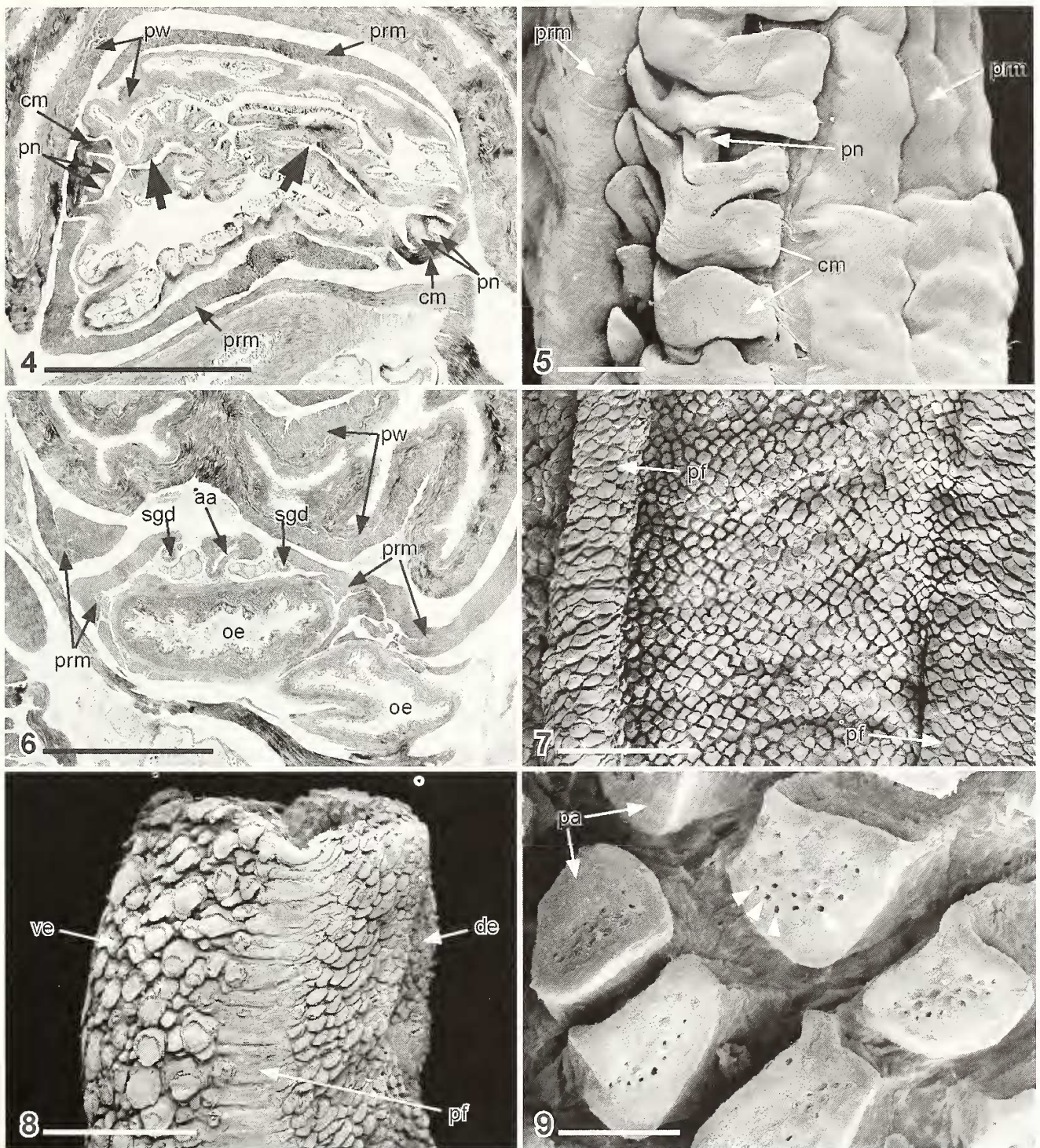
Figures 4–9. Proboscis of *Ficus subintermedia*. **4.** Transverse histological section through introverted proboscis, note pseudo dorsal folds formed by proboscis wall (large arrows). **5.** SEM image of exterior wall of introverted proboscis. **6.** Transverse histological section through haemocoel anterior to nerve ring, with proboscis retractor muscles attaching to esophagus. **7.** SEM image of interior wall of introverted proboscis, dissected by longitudinal incision in ventral surface, showing papillose surface. **8.** SEM image of lateral exterior wall of everted proboscis tip. **9.** SEM image showing detail of epithelium lining proboscis wall, pores in papilla (**pa**) are marked with white triangles. Abbreviations: **aa,** anterior aorta; **cm,** circular muscle; **de,** dorsal epithelium; **oe,** esophagus; **pa,** papilla; **pf,** proboscis fold; **pn,** proboscis nerve; **prm,** proboscis retractor muscle; **pw,** proboscis wall; **sgd,** salivary gland duct; **ve,** ventral epithelium. Scale bars: Figures 4, 6–8 = 1 mm; Figure 5 = 250 μm; FIGURE 9 = 50 μm.
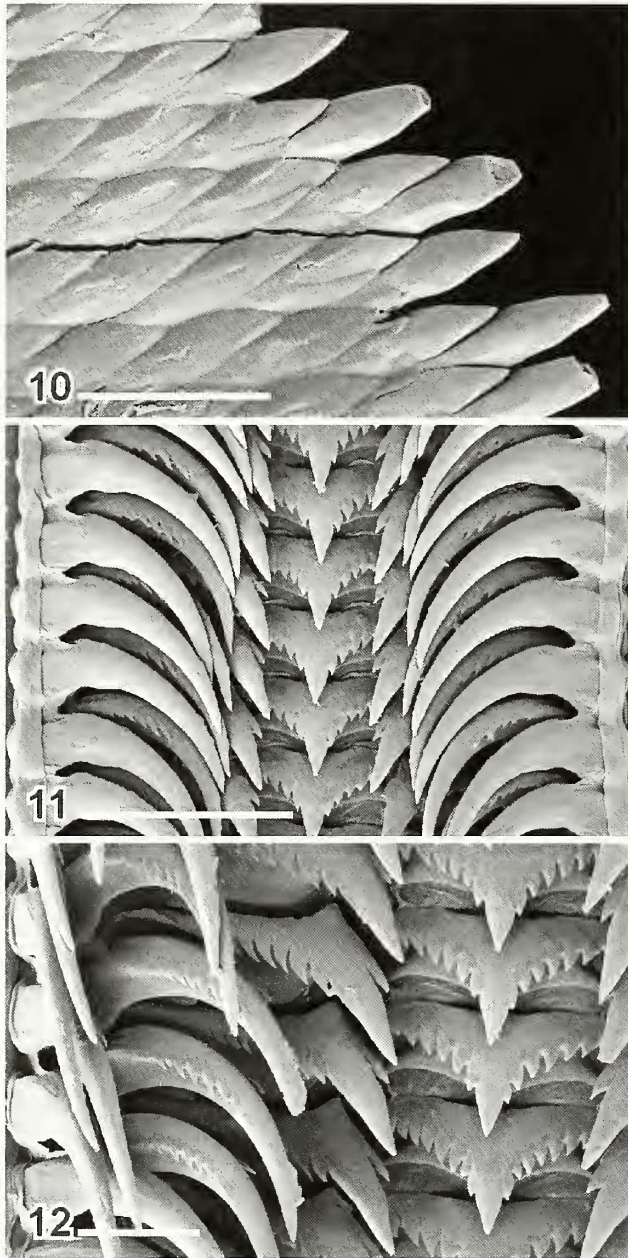
Figures 10–12. SEM images of the jaws and radula of *Ficus subintermedia*. **10.** Detail of jaw composed of rods. **11.** Radula. **12.** Detail of radular teeth. Scale bars: Figures 10, 12 = 100 μm; Figure 11 = 250 μm.

proboscis can be reassessed as potential synapomorphies. Densely-packed teeth on the field radula were postulated as an intermediate between the taenioglossan and stenoglossan radular patterns (Riedel, 1994). However, the radular dentition of *Ficus subintermedia* is very similar to that of tonnoidean and other higher caenogastropods (Warén and Bouchet, 1990; pers. observ.) and is not remarkable (Table 1).

The introversion (turning inside out) of the proboscis was correctly identified by Riedel (1994) as a character differentiating Tonnoidea and Ficoidea, as the tonnoid
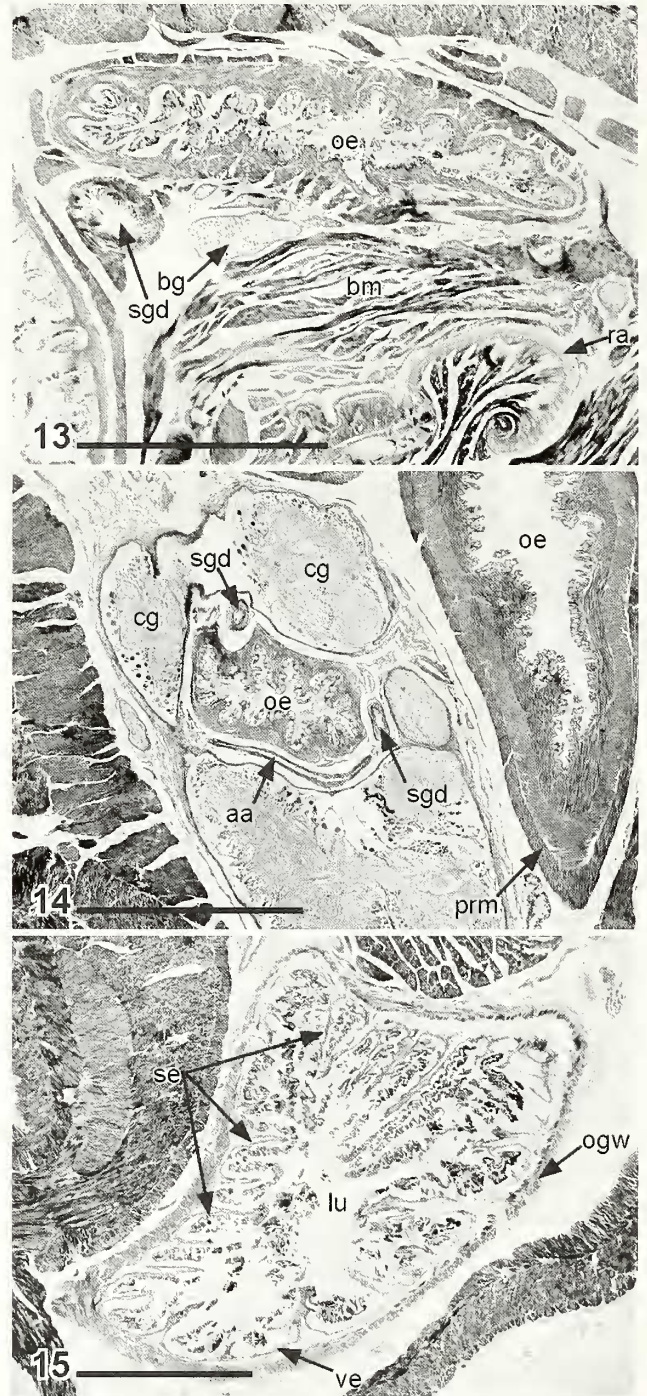

Figures 13–15. Histological sections through the esophagus of *Ficus subintermedia*. **13.** Oblique section through anterior esophagus adjacent to buccal mass. **14.** Transverse section through esophagus and circumesophageal nerve ring. **15.** Transverse section through esophageal gland. Abbreviations: **aa,** anterior aorta; **bg,** buccal ganglia; **bm,** buccal mass; **cg,** cerebral ganglion; **lu,** lumen; **oe,** esophagus; **ogw,** esophageal gland wall; **prm,** proboscis retractor muscle; **ra,** radula; **se,** septum; **sgd,** salivary gland duct; **ve,** ventral epithelium. Scale bars = 1 mm.
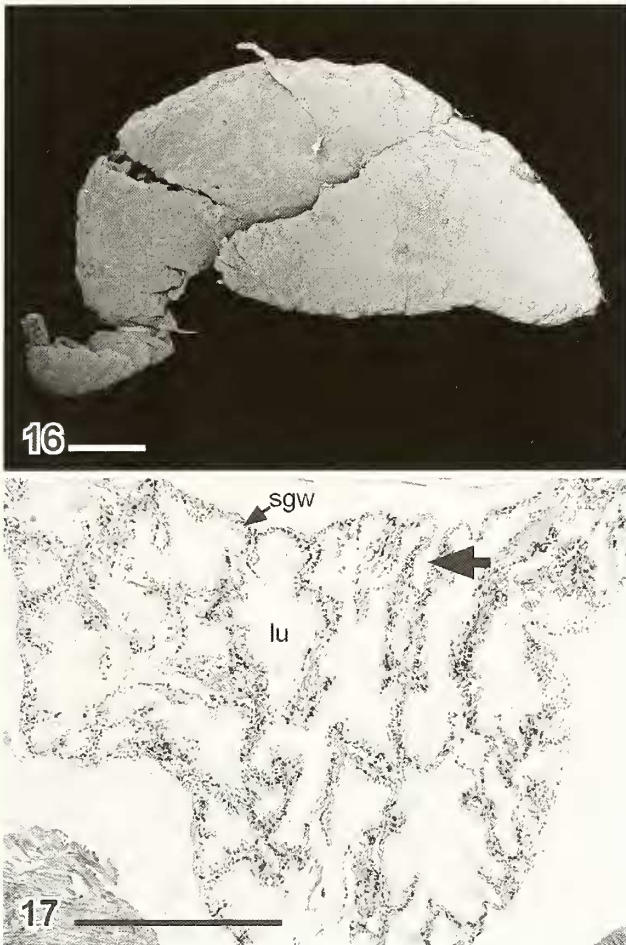
Figures 16–17. Salivary gland of *Ficus subintermedia*. **16.** SEM image of bilobed salivary gland. **17.** Histological section through salivary gland, note incomplete separation between lobes marked with a large arrow. Abbreviations: **lu,** lumen; **sgw,** salivary gland wall. Scale bars = 500 m.

proboscis is retractile but can not truly be introverted (Day, 1969; Simone, 1995) (Figures 20, 21, Table 1). However, introversion is a feature of the acrembolic proboscis of several other distantly related caenogastropod groups (including naticoids and ptenoglossans) as well as the pleurembolic proboscis of Neogastropoda, and could not alone be considered a potential synapomorphy. The superficial similarities between the ficid and conoidean proboscis, discussed above, are inconclusive.

A comparison between Ficidae, Tonnoidea, and Neogastropoda shows that there are few potential synapomorphies (Table 1). A pair of dorsal jaws, composed of rods, is present at the anterior margin of the buccal mass of *Ficus subintermedia*. These are alike in position and composition to those of *Tonna galea* (Weber, 1927) and most other middle caenogastropods (Strong, 2003), while paired jaws are not present in neogastropods (Strong, 2003). But as jaws are plesiomorphic in Caenogastropoda, they are not informative in assessing the monophyly of Ficidae with Tonnoidea or Neogastropoda.
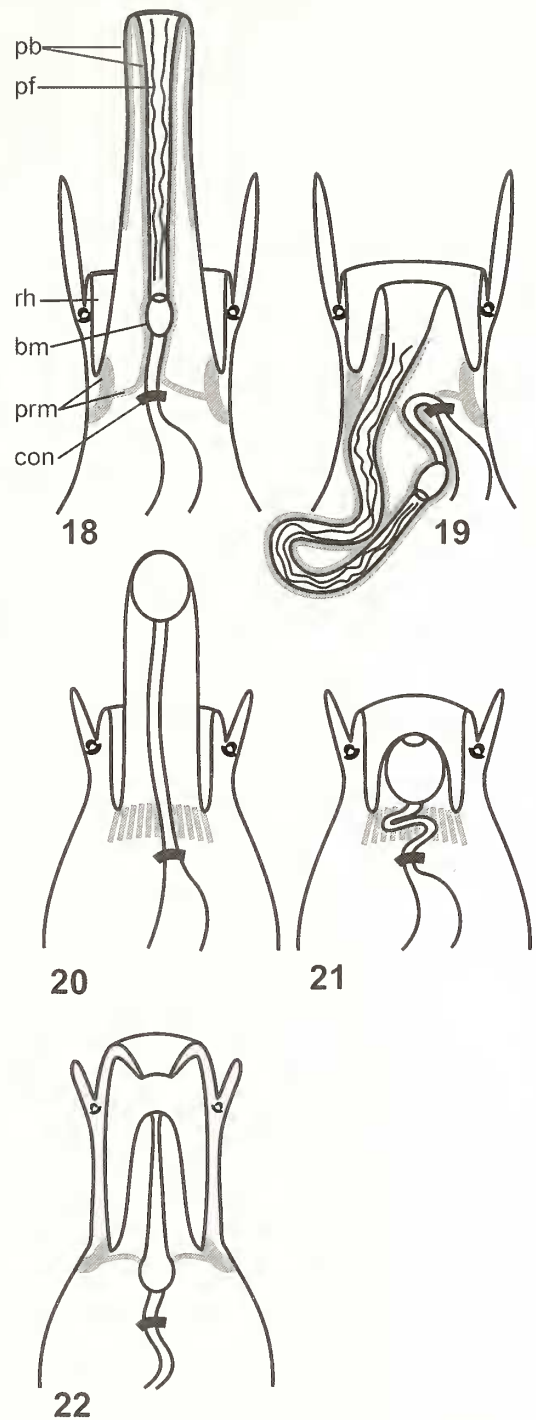
Figures 18–22. Diagrammatic representations of proboscis configuration, with proboscis retractor muscles shaded grey. Salivary glands are not illustrated. **18, 19.** *Ficus subintermedia* **18.** Proboscis everted. **19.** Proboscis introverted. **20, 21.** A tonnoidean, modified from Day (1969). **20.** Proboscis everted. **21.** Proboscis introverted. **22.** Terebridae (Conoidea), with intraembolic proboscis, modified from Simone (1999: fig. 27). Abbreviations: **bm,** buccal mass; **con,** circumesophageal nerve ring; **pb,** proboscis; **pf,** proboscis fold; **prm,** proboscis retractor muscle; **rh,** rhynchodeum. Not to scale.

Table 1. A comparison of the main features of the proboscis and foregut of Ficidae, Tonnoidea and Conoidea, using information available in the literature (see text for references).

Foregut Anatomy	Ficidae	Tonnoidea	Conoidea
Proboscis	Very long, acrembolic	Moderately long, contractile, not introvertable	Various lengths and forms, including intraembolic, pleurembolic, reduced/absent
Proboscis lumen (when introverted)	With pseudo dorsal folds	Not applicable as proboscis does not introvert	Simple
Proboscis retractor muscles	Attaching to proximal proboscis wall and esophagus, sheathing anterior esophagus, buccal mass and distal proboscis	Short, attaching to proximal proboscis wall	Attaching to interior of proboscis wall, also attaching to buccal mass in some taxa (Terebridae)
Permanent (external) rhynchodeum	Present	Present	Present, introvertable in some taxa
Buccal mass	Small	Large	Variable, reduced/absent in some taxa
Jaws	Paired dorsal jaws present, composed of rods	Paired dorsal jaws present, composed of rods	Jaws absent
Radula	Taenioglossan	Taenioglossan	Variable, 5 or fewer teeth, absent in some taxa
Salivary glands	Single pair of small salivary glands; bilobed, homogeneous	Single pair of salivary glands plus proboscis glands derived from salivary glands (except Personidae)	Salivary glands usually present, accessory salivary glands present in some taxa
Anterior esophagus	Dorsal and ventrolateral folds absent	Prominent dorsal and ventrolateral folds present	Ventrolateral folds absent, dorsal folds reduced or absent
Esophageal gland	Open lumen with few septate folds, low glandular epithelium, confluent with esophagus	Dense septate folds, tall glandular epithelium, confluent with esophagus	Tubular venom gland, with tall glandular epithelium and muscular bulb

Salivary gland form varies considerably between caenogastropods, with a pair of accessory salivary glands present in many neogastropods and an extremely large pair of acid-secreting proboscis glands, derived from the salivary glands, present in tonnoids (except Personidae) (Weber, 1927; Simone, 1995; Andrews et al., 1999) (Table 1). The anterior (acinous) and posterior (acid-secreting, proboscis) salivary glands of *Cymatium intermedius* have distinct histologies reflecting their specialized functions (Andrews et al., 1999). Although the salivary glands of *F. subintermedia* are superficially bilobed, the histology is homogeneous. The salivary glands of tonnoideans and other caenogastropods are typically composed of large cells with narrow lumens (Andrews et al., 1999). The salivary glands of *F. subintermedia* are unusual in that they are dominated by an expanded lumen, perhaps for storing saliva. The absence of either accessory salivary glands or proboscis glands is uninformative in establishing the relationship of *Ficus* to either Tonnoidea or Neogastropoda.

Modification of the esophageal gland to form a discrete organ, the gland of Leiblein or its partial homologue the venom gland (Ponder, 1970), is a feature common to most neogastropods. Unlike most other caenogastropods including Tonnoidea, the esophageal gland of *Ficus subintermedia* was poorly developed and formed a sac-like expansion of the esophagus (Table 1).

The digestive properties of the ficid esophageal gland are entirely unknown.

Ficids display a variety of morphological synapomorphies which, at this stage of our knowledge of caenogastropod anatomy, confound attempts to affiliate the group with other higher caenogastropods. Some aspects of proboscis morphology, together with the simplified esophagus and reduced buccal mass, could be seen as suggesting an association with Neogastropoda. Comparisons between taxa are helpful for elucidating homology, but the phylogenetic affinities of Ficidae require further investigation using cladistic methodology, and given their unusual morphology, with a particular focus on molecular data.

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